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ABSTRACT

Linguistics has chosen as its niche the language component of human communication and, naturally enough, the neurolinguist has concentrated on lateralized language systems of the cerebral hemispheres. However, decoding a speaker's total message requires attention to gestures, facial expressions, and prosodic features, as well as other somatic and visceral nonverbal communication channels over and above the sentences uttered. Speech is normally produced within a matrix of behavior patterns output both by intentional and by automatic nonverbal communication systems. The neural structures responsible for this nonlinguistic communication develop early in human ontogeny and evolved in phylogeny before language. To fully understand language and its neural substrata, the scope of the neurolinguist's concern must be broadened to include the entire range of subcortical and cortical systems responsible for human communication of all types and levels. Especially relevant is the "limbic system," a forebrain complex shared homologously by all mammals. In the first year of postnatal life the human infant develops several types of limbically based communication patterns. In adults, limbic communication systems and limbically regulated social and emotional behavior patterns integrate with symbolic, propositionally based linguistic behavior of the left hemisphere mediated by specialized systems of the right hemisphere. This paper presents an overview of the anatomical structure of the limbic system and a summary of past proposals for the functional organization of limbic information processing systems. Citing both experimental work on limbic involvement in primate social communication and clinical evidence on limbic involvement in various types of human neural dysfunctions, a framework will be presented within which the relationship of limbic and linguistic communication may be considered. (Author)

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THE ROLE OF THE LIMBIC SYSTEM IN HUMAN COMMUNICATION*

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Recent investigations into the neurological substrata of language processing have tended to emphasize two areas of empirical research: first, the pathology and symptomology of language disorders, and secondly, the lateralization of language functions to one or the other cerebral hemisphere. Common to both interests has been an almost exclusive concern for the neocortical systems of the brain and for language and speech. Reasonable as this may seem, such a focus actually provides too narrow a theoretical foundation because grammatically organized, phonologically structured verbal encodings of messages happens to be only one of many levels and types of human communication. Extralinguistic and nonverbal aspects of communication aren't mere window-dressing optionally accompanying sentences, but a fundamental ingredient of the process by which people encode and decode messages. Many propositional and symbolic components of communicative interactions aren't expressed by linguistic means, but rather by conventionalized manual gestures, facial expressions, body movements, and prosodic elements beyond phonology. This symbolic activity cannot be considered linguistic in any strict sense, although from the point of view of the neural systems responsible for propositional communication, they are likely to be merely alternative output modes to speech and based on neural processes at the same level. Over and above these propositional nonverbal communication schemata, there are still other forms of NON-propositional multimodal behavior patterns that communicate. Some are output automatically under specified internal or external conditions and others are produced intentionally. Both are the product of neural elements other than the neocortical speech systems neurolinguists have fixed their attention on.

The obvious candidate for the level of brain organization likely to be

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*Read before the Winter 1975 Meeting of the Linguistic Society of America

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controlling the bulk of non-propositional human communication is the limbic system. This forebrain network of cortical and subcortical structures is often thought of only in terms of its regulation of emotion and motivation, but in fact its range of functional responsibilities is quite large and includes major segments of our social and communicative behavior. It is known that we share these systems homologously with other mammals, and that for infrahuman primates the limbic system is the highest level of neural activity responsible for species-specific communication systems. Up to some point in ontogenetic development it is the limbic system of the infant that controls social and communicative interactions with those in the environment. Furthermore, the vast majority of the limbic functions acquired by the infant remain part of the adult communication repertoire as a neurobehavioral framework into which linguistic communication is embedded. There can be no doubt that the limbic system plays a strong role in human communication of all types, and while there are huge literatures on both the limbic system and on human communication, surprisingly little attention has been paid to the intersection of these two areas of research.

What I would like to do here is help rectify this unprofitable neglect by presenting a brief overview of the limbic system, summarizing some tentative conclusions about social and communicative functions of limbic subsystems and their integration with both higher and lower levels of forebrain activity in human beings. Because of time constraints I will be unable to present specific justification for many of these conclusions and I won't be able to say much at all about limbic anatomy and physiology. You are referred to the handout material and particularly the bibliography on the last page for access to further information.

Examining the brains of modern vertebrates, one finds a close relationship between olfactory systems and visceral regulatory mechanisms of the forebrain.

The two functional domains are integrated in the form of the rhinencephalon, or 'nose-brain,' the subcortical components of which are illustrated on page 2 of the handout. Although a great many changes have taken place in the evolution of the mammalian brain, including drastic repositionings of rhinencephalic structures, components of the human rhinencephalon retain approximately the same functional interrelations as for other mammals. In the 19th century the rhinencephalon was assumed to be involved only in olfactory processing and, with the rise in importance of vision among primates, it is true that basic olfactory structures of the rhinencephalon decrease in size and importance. However, the much greater expansion of the neocortex obscures the fact that major components of the rhinencephalon become increasingly more elaborate in the ascending primate scale. For example, the human hippocampus is four times as large as that of a hypothetical basal insectivore of the same size and more than twice as large as that of a gorilla. Particularly striking in mammalian evolution has been the elaboration of CORTICAL structures within the rhinencephalon. The two most basic types of cortex are the PALEOCORTEX as found in the prepyriform region and the ARCHICORTEX characteristic of the hippocampus. All other cortex arose phylogenetically and differentiates ontogenetically in concentric growth rings outward from these two points of origin. Certain aspects of the evolution of cortical components of the primate rhinencephalon may be inferred from page 3 of the handout and their modified recapitulation in human embryological development may be seen on page 4.

A theoretical landmark in limbic research was the famous proposal of Papez (1937) establishing the role of a network of rhinencephalic structures in emotion. Initially, the emphasis was on the visceral regulatory functions of the structures in the "Papez circuit," summarized in A on page 5 of the handout, and it is in this context that MacLean (1949) applied the label "visceral brain." Meanwhile,

evidence was accumulating that the functional activity of these structures was actually much broader than this. A second major landmark was Pribram and Kruger (1954), summarized in D on page 5, in which three anatomically definable subsystems of the "olfactory brain" were distinguished. Along the way, Pribram and Kruger related these structures to the roles they play in nonvisceral domains such as arousal, learning, and social behavior. The phrase "limbic system" was coined by MacLean (1952), the term "limbic" itself being borrowed from Broca, who in 1878 had identified the ring of forebrain structures surrounding the mammalian brain stem as "*le grand lobe limbique*" from the Latin *limbus* meaning 'border or rim.' The shift in terminology helped establish these forebrain mechanisms as a general information processing system that is, in a sense, an entire brain in itself, participating in most neurofunctional domains. The first indication of limbic involvement in communication came from Smith (1941), work showing that electrical stimulation of anterior cingulate cortex elicited overt vocal activity in monkeys.

Over the past 30 years, a mountain of data on the limbic system has been generated and a reasonable consensus has been reached on which structures should be included in it. Page 6 of the handout diagrammatically represents limbic components and indicates for the cortical structures whether they are derivatives of the anterior parapyriform moitié or the posterior parahippocampal moitié. While much has been discovered about efferent and afferent fiber connections between limbic structures, this information has not been very helpful in tracing out a functional wiring diagram of limbic subsystems since practically everything is reciprocally connected to practically everything else; notice page 7 of the handout. Electrical stimulation of subcortical nuclei of the limbic system triggers a long list of overt behaviors, most of them elicitable from a large number of different structures. Page 8 of the handout gives a partial look at the

behaviors elicited by amygdaloid stimulation in the cat. Lesioning and ablation studies have produced no evidence of functional lateralization for limbic processing, and ordinarily bilateral lesions are necessary to produce any noticable behavioral deficits.

In all of us mammals, the limbic system is demonstrably involved in the control of multimodal behavior sequences that serve as signs for particular internal motivational states of fear, alarm, surprise, rage, and so on. These sign complexes constitute the overwhelming majority of messages in the communication repertoires of infrahuman primates and are easily observable in human behavior. Limbic structures are also involved in the production and recognition of a second class of messages, those regulating social interactions involving territoriality, friendly and submissive gestures, dominance relations, agonistic displays, mother-infant interactions, and male-female relations. Research investigating the role of limbic structures in mammalian social behavior has perhaps been carried out most productively by R.E. Myers and his collegues. From this work emerges the conclusion that it is especially prefrontal cortex and to a lesser degree anterior temporal cortex that controls social interactions. Bilateral lesions in these regions, but not in cingulate or visual association cortex, produce severe and lasting deficits in maternal behavior, position in the dominance hierarchy, and general level of social involvement.

Since Smith's work, the role of anterior cingulate cortex and other limbic regions in primate vocal activity has been investigated by a number of researchers, for example, Robinson, and Ploog and his associates. In this research, however, there has often been a tendancy to inadequately distinguish in a formal way between vocal activity in general, vocal components of multimodal sign complexes output automatically in particular motivational states, species-specific vocal components of social regulatory behavior, and the learned vocalizations of individuals.

All four types of vocal activity may be expected to find a common neurological substratum in midbrain centers known to control vocalizations, but beyond this, they are almost certainly realized quite differently in various limbic subsystems. The entire vocal call repertoire of squirrel monkeys may be elicited by limbic stimulation, the elicited calls triggering appropriate responses from other members of the species. Page 10 of the handout identifies the sites from which the cackling call of squirrel monkeys were elicited by Jürgens and Ploog (1970), but, since the actual site stimulated is incapacitated during stimulation, the response is actually produced by regions this point projects to. This makes it very difficult to draw any firm conclusions about the location of the structures most directly controlling this activity. We know that in our species control functions over complex intentional vocalizations have shifted upwards to higher levels of neural organization; most notably Area 4, the primary motor cortex, and for phonologically structured vocal output, Broca's area in the dominant hemisphere. These neocortical systems are not involved in the species-specific call systems of monkeys, although stimulation of primary motor cortex elicits movements of laryngeal muscles. Bilateral ablation of either Area 4 or the closest homologue of Broca's area in monkeys has no effect on vocal activity whatsoever, although Sutton has shown that bilateral removal of anterior cingulate cortex does result in the weakening or loss of learned vocalizations.

Obviously it would be beneficial to have some explicit understanding of the organization of the limbic system into the subsystems relevant to particular domains of communicative activity. Unfortunately, with only a few exceptions, limbic researchers have dealt exclusively with the functions of single structures and have had almost nothing to say about the limbic system as a whole. Only two major proposals have been put forth claiming to define functionally relevant limbic subsystems: the already mentioned division of Pribram and Kruger (1954) and the

three-way classification of MacLean (1973) dividing the limbic system into a lower subsystem fed by the amygdala; a subsystem connected by the septum; and a cingulate subsystem with strong visual input. I would like to suggest a modified framework for viewing limbic organization, one that is specifically relevant to communication functions. To do this it will be helpful to consider limbic activity in the context of a lower striatal level, as well as a higher neopallial level of forebrain organization approximating MacLean's distinction between the reptilian forebrain, the paleomammalian brain, and the neomammalian brain. Page 1 of the handout outlines a preliminary division of the limbic system into four subsystems operating at three levels, and sketches the functional relations of these subsystems at five levels of forebrain organization.

The striatum is the first subdivision of the vertebrate telencephalon, and activity at this level is characterized by reflexive, stereotyped responses to a limited range of stimuli related to basic matters of survival. As defined here, the striatal system is meant to incorporate subordinate midbrain and brain stem systems in what amounts to a hierarchical metasystem. The higest level communication functions of reptiles and birds are carried out by specialized striatal systems, but in mammals there is only a minimal involvement of the striatum in communicative activity, at a level that might be called primary sign behavior. In human ontogeny, the earliest behavior with even a marginal claim to the label "communicative" is the global crying of the neonate, triggered by the reticular formation as a total somatic mobilization in response to any type of discomfort stimulus.

The first level of limbic activity corresponds roughly to what Pribram and Kruger identified as the RHINAL SYSTEM, based anatomically on the septum, diagonal band, and particularly the hypothalamus as it receives olfactory and other input and regulates autonomic and endocrine activity related to self-preservation;

see page 11 of the handout. The appetitive subsystem is the basis for internal sensations and associated drive states of hunger, thirst, pain, rage, and so on. Ontogenetically, this subsystem becomes relevant to the communication sphere at about two weeks postnatally with the onset of differentiated crying, soon leading to an identifiably different hunger cry, rage cry, and pain cry. In adults, this subsystem controls a large set of multimodal, mostly visceral sign complexes that may be used by other members of the species to infer the motivational state of the individual in question.

The first subsystem at the second level of limbic activity corresponds to Pribram and Kruger's PALEOL SYSTEM, being based on mostly anterior rhinencephalic components possessing mostly motor/output processing functions. The anterior cingulate juxtallocortex and the amygdala are of particular importance here. Functionally, this level of limbic activity is related to behavior sequences fostering species survival and represents a more efficient means of implementing reactions to both internal appetitive states and external environmental stimuli. Activity at this level has been characterized by Pribram as involving the Four F's: feeding, fighting, flight, and reproduction. Ontogenetically, this subsystem is the means of the infant's assimilation into a network of social relationships based on a variety of instinctual interactions such as the establishment of the primary attachment with the mother, and the special attention paid to the human face and voice. In the vocal sphere, it is probably this subsystem that is responsible for the development of a new class of comfort sounds from about 6-8 weeks postnatally that contrast sharply with the previously existing discomfort vocalizations.

The second affective subsystem corresponds roughly to Pribram and Kruger's HIPPOCAMPAL-CINGULATE SYSTEM, and is based on the activity of the posterior

cingulate juxtallocortex, the hippocampus and related schizocortical regions (see page 12 of the handout). This subsystem has mostly sensory/input processing functions, receiving input from all sensory modalities and permitting instrumental learning based on memory functions of the hippocampus. Emotions develop here as a new level of internal experience produced by the integrated activity of the two affective subsystems. The learning made possible by this level of the limbic system becomes the basis for making the responses of the individual more appropriate to both the immediate physical and social context. For the human infant, this subsystem is not so much the direct basis for overt communicative behavior as it is for learning about the affective content of other people's behavior. It is at this point in development that the child will cry when addressed in a harsh voice and be soothed by a pleasant tone. In adults, it is possible that the posterior affective subsystem has the responsibility of tracking the affective state of those we interact with.

The third level of limbic activity was not distinguished by either Pribram and Kruger or MacLean, perhaps because it is found only in the higher primates and their data was derived mostly from rats, cats, and monkeys. Anatomically, its basis within the limbic system is obscure, and its status therefore only tentative, but it presumably involves the highest levels of juxtallocortex and proisocortex; in particular the orbitofrontal and anterior temporal cortex and the areas of the anterior cingulum transitional to the primary motor cortex of Area 4. Justification for positing the existence of this subsystem comes from data on the attainment by humans, and to a much lesser degree the higher apes, of volitional control over the implementation of behavioral subroutines. In human ontogeny, voluntary control over motor output begins to develop from about 3-4 months as the child begins mastering complex action schemata as a means of satisfying affective goals such as the desire for an object. At some point, limited control

over affective output patterns themselves is achieved, enabling the child to evince many of the overt signs of anger without really being angry. From about 8-9 months, the child begins to intentionally use learned prosodic features, especially intonation contours, to communicate affective states, thereby meeting Morris' definition of signal communication as the intentional use of signs. At about 10 months the child begins to imitate and repeat sounds, further evidence of the increasing degree of voluntary control over vocal output mechanisms, an accomplishment other primates can match only to a very limited extent. It is during this same period that children begin using an apparently universal set of four word-like utterances (for example the food-hunger form "mam") that don't seem to be based on the neocortical systems controlling babbling.

As neopallial systems arose phylogenetically and develop ontogenetically, they inhibit certain limbic functions and carry them out at a higher level in a novel fashion. Nonetheless, each limbic subsystem continues to exercise control over its sphere of human activity as a subordinate component of the higher neopallial metasystem. With the rise of cognitive processing in the human infant from about 12 months, a new level of communicative competence is achieved as the child intentionally uses symbolic multimodal gesture complexes to communicate propositional messages. These gestural patterns and the verbal and linguistic systems that soon follow take their place within the hierarchy of forebrain communication functions, with each higher level being built upon the foundation of the systems below it. Communication functions of the brain, therefore, are best viewed as distributed over this entire hierarchy. Overt verbal and nonverbal communicative behavior patterns must be parcelled out among the various levels of internal functional systems according to what in the sender was responsible for producing them and what in the receiver is responsible for recognizing them.

A complication in this parcelling out of functional responsibilities is introduced at the neopallial level by the lateralization of functional capabilities taken over from the limbic system. While I hesitate to contribute to the growing cult of the right hemisphere, the evidence indicates that the nondominant hemisphere bears a special relationship to subordinate affective subsystems, while the dominant left hemisphere acts in a mostly inhibitory fashion with respect to affective functions. Voluntary control over the output of propositional communication schemata and the elaboration of sensory input by verbal encodings of conceptual information structures seem to be basically left-brain functions. The right hemisphere appears to elaborate limbically generated input in such a way that it retains its immediateness and rich affective value. Various people have claimed that the right hemisphere is more 'emotional' than the left, and the reason for this, if true, would have to involve a qualitatively different right-brain interaction with the limbic system.

It has long been noted by clinicians that patients with left-sided cerebral lesions tend to be more emotionally volitile than patients with right-sided lesions, the latter tending to be curiously indifferent to their disorder, often denying its existence or making inappropriate jokes about it. Gainotti (1972) confirmed these informal observations, citing corroborative evidence that pharmacological deactivation of the left hemisphere often leads to catastrophic-depressive reactions not found with deactivation of the right. If the left hemisphere acts to inhibit either right hemisphere elaborations of limbic functions or the limbic system directly, the emotional lability of left-lesioned patients would be explicable as the partial release of limbic functions from this inhibitory control. Right-lesioned patients, because of impaired limbic functions at the neopallial level, would tend to have less conceptual consciousness of the emotional implications of their disorder and perhaps for this reason be relatively

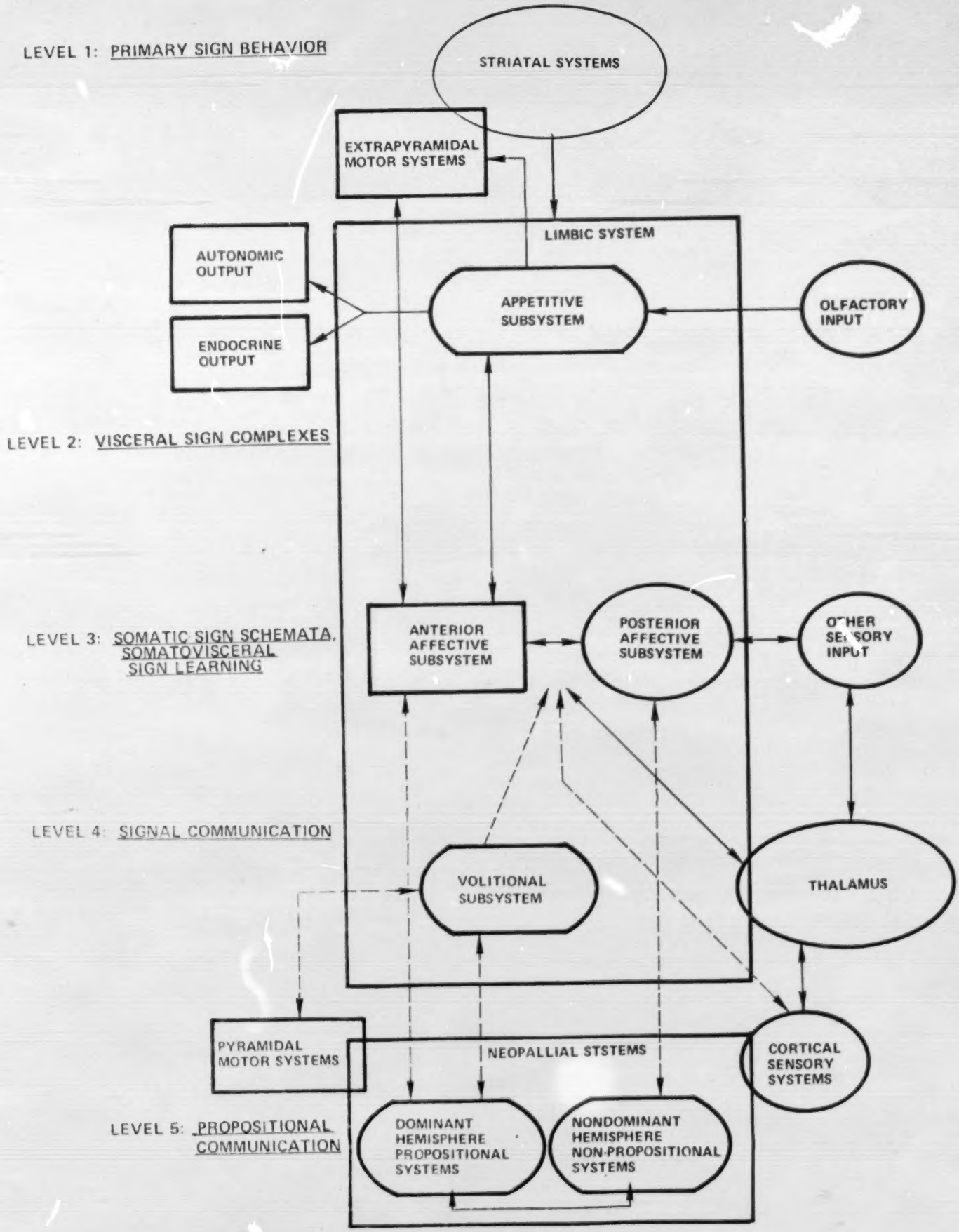
indifferent toward it. The possibility of a disjunction between conceptual awareness in the left hemisphere versus the representation of emotional significance in the right stands out clearly from the work of Sperry and Gazzaniga (1967) in which a picture of a nude was flashed to the right hemisphere of a split brain patient while objects to be named were flashed to the left. A sneaky grin crept across the patient's face, but he was unable to conceptualize any reason why such a reaction should be taking place in his body. There is some evidence that the integration of the two domains is accomplished by frontal lobe systems that may or may not be part of the limbic system proper, this notion perhaps being testable in those many split brain patients in whom the genu of the corpus callosum has been left intact.

It is known that prosodic components of speech and emotional interjections often function as a running commentary on the affective import of the verbally encoded segmental content of speech. Further support for a claim that the right hemisphere is carrying out specialized limbic-related functions comes from a dichotic listening study of King and Kimura (1972) showing a left-ear superiority for processing laughter, coughing, crying, and other nonspeech vocalizations. Milner (1962) found that patients with right temporal lobectomies, but not left, have significant deficits in the processing of tonal patterns. While neither the clinical nor the experimental evidence is sufficient to support a statement of exactly what the right versus the left hemisphere is doing with respect to limbic functions, there are strong indications of differential processing in the two hemispheres. It may turn out that the right hemisphere is the mediator between the store of verbally encoded conceptual information in the dominant hemisphere and the motivational-appetitive mechanisms of the limbic system.

To determine the facts in this matter, and more generally to understand communication functions of the limbic system, it will be especially important to gather data from those human clinical syndromes with a specifically limbic etiology. Because of time limitations, I can only list a few of those disorders that might prove instructive in this regard: (1) congenital and acquired arhinencephaly producing what Gascon and Gilles called "limbic dementia;" (2) Gilles de la Tourette's syndrome, whose major symptoms are body tics, barks and grunts, and compulsive obsenities; (3) Temporal lobe epilepsy, known to involve the amygdala and nearby schizocortical regions of the temporal lobe; (4) Psychosurgery victims with prefrontal lobotomies, cingulotomies, and amygdalotomies suffering from impaired emotional responsiveness, loss of self-awareness, loss of emphathy and judgement; (5) Early Infantile Autism, whose symptoms clearly suggest a disorder of limbic functions related to social interaction, arousal, and habituation.

Very little systematic knowledge exists about limbic manifestations in human linguistic communication in the normal adult, but there are many points of contact between the study of limbic processing and neocortical language functions that deserve to be investigated. Particularly interesting are emotional speech, obscene and vulgar speech, and speech under stress; all of which may be retained in aphasic disorders that otherwise disrupt language performance. The force of the connection between limbic and linguistic processing is dramatically illustrated in B.W. Robinson's description of a Broca's aphasic paralyzed on the right side of the body. The patient became manic depressive and when he was in the manic phase, the language disorder and paralysis both disappeared, only to reappear whenever medication was administered. In a normal individual, speech under stress may resemble that of a Broca's aphasic and it is literally possible to become speechless with rage as control functions over behavior shift down from

propositional neopallial systems to limbic subsystems in interactional situations involving the Four F's. Upon sitting on a tack, it is likely to be the limbic system that controls the vocal and nonvocal reaction, and if words are uttered at all, they are often obsenities that somehow manage to carry a limbic 'charge.' If someone calls you a dirty name, it is irrelevant whether your parents were really married or not; the insult was not aimed at the neocortex, but lower down. Similarly, neurolinguists should lower their sights from neocortical speech systems to encompass limbic subsystems that play a major role in human communication.

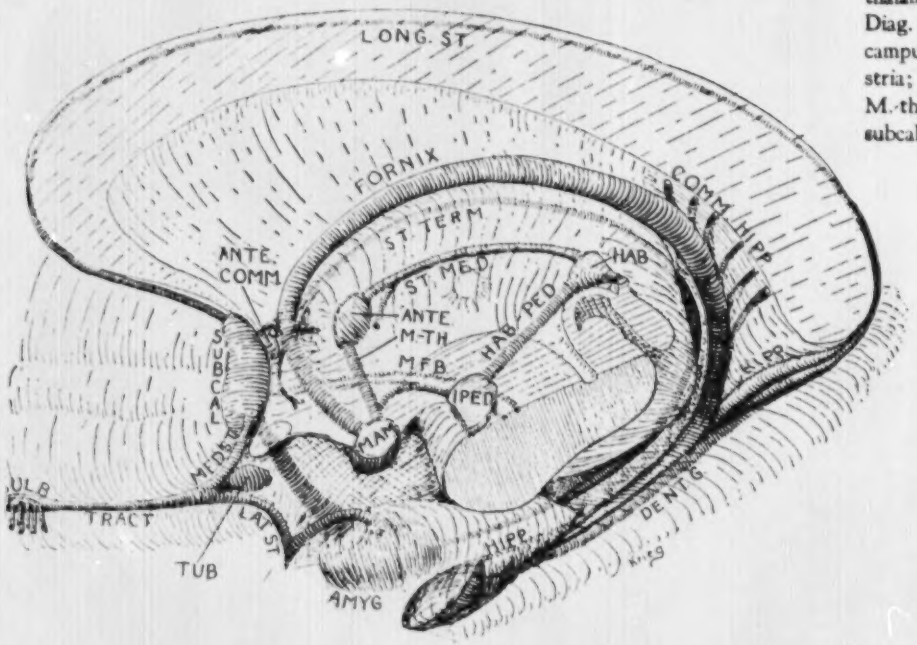

LEVEL 1: PRIMARY SIGN BEHAVIOR
STRIATAL SYSTEMS
EXTRAPYRAMIDAL MOTOR SYSTEMS
LIMBIC SYSTEM
AUTONOMIC OUTPUT
ENDOCRINE OUTPUT
APPETITIVE SUBSYSTEM
OLFACTORY INPUT
LEVEL 2: VISCERAL SIGN COMPLEXES
LEVEL 3: SOMATIC SIGN SCHEMATA, SOMATOVISCERAL SIGN LEARNING
ANTERIOR AFFECTIVE SUBSYSTEM
POSTERIOR AFFECTIVE SUBSYSTEM
OTHER SENSORY INPUT
LEVEL 4: SIGNAL COMMUNICATION
VOLITIONAL SUBSYSTEM
THALAMUS
PYRAMIDAL MOTOR SYSTEMS
NEOPALLIAL STSTEMS
CORTICAL SENSORY SYSTEMS
LEVEL 5: PROPOSITIONAL COMMUNICATION
DOMINANT HEMISPHERE PROPOSITIONAL SYSTEMS
NONDOMINANT HEMISPHERE NON-PROPOSITIONAL SYSTEMS

TWO VIEWS OF THE HUMAN RHINENCEPHALON

(Adapted from Krieg, 1966: 345, 346)

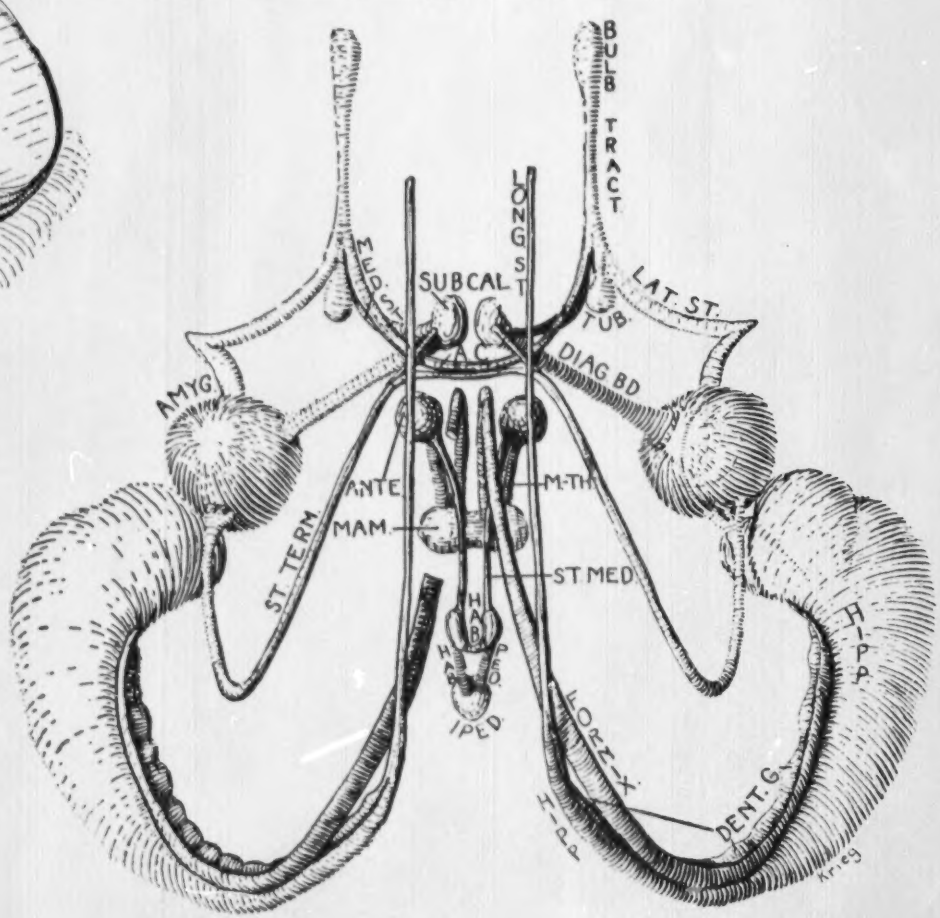
A. Reconstruction of human rhinencephalon, as seen in a ventromedial view of the right cerebrum.

Amyg., amygdala; Ante. Comm., A.C., anterior commissure; Ante., anterior nucleus of thalamus; Bulb, olfactory bulb; Comm. Hipp., hippocampal commissure; Dent.G., dentate gyrus; Diag. Bd., diagonal band; Hab., habenula; Hap-ped., habenulopeduncular tract; Hipp., hippocampus; Iped., interpeduncular nucleus; Lat.St., lateral olfactory stria; Long. St., longitudinal stria; Mam., mammillary body; Med.St., medial olfactory stria; M.F.B., medial forebrain bundle; M.-th., mammillothalamic tract; St.Med., stria medullaris; St.Term., stria terminalis; Subcal., subcallosal gyrus; Tract., olfactory tract; Tub., olfactory tubercle.

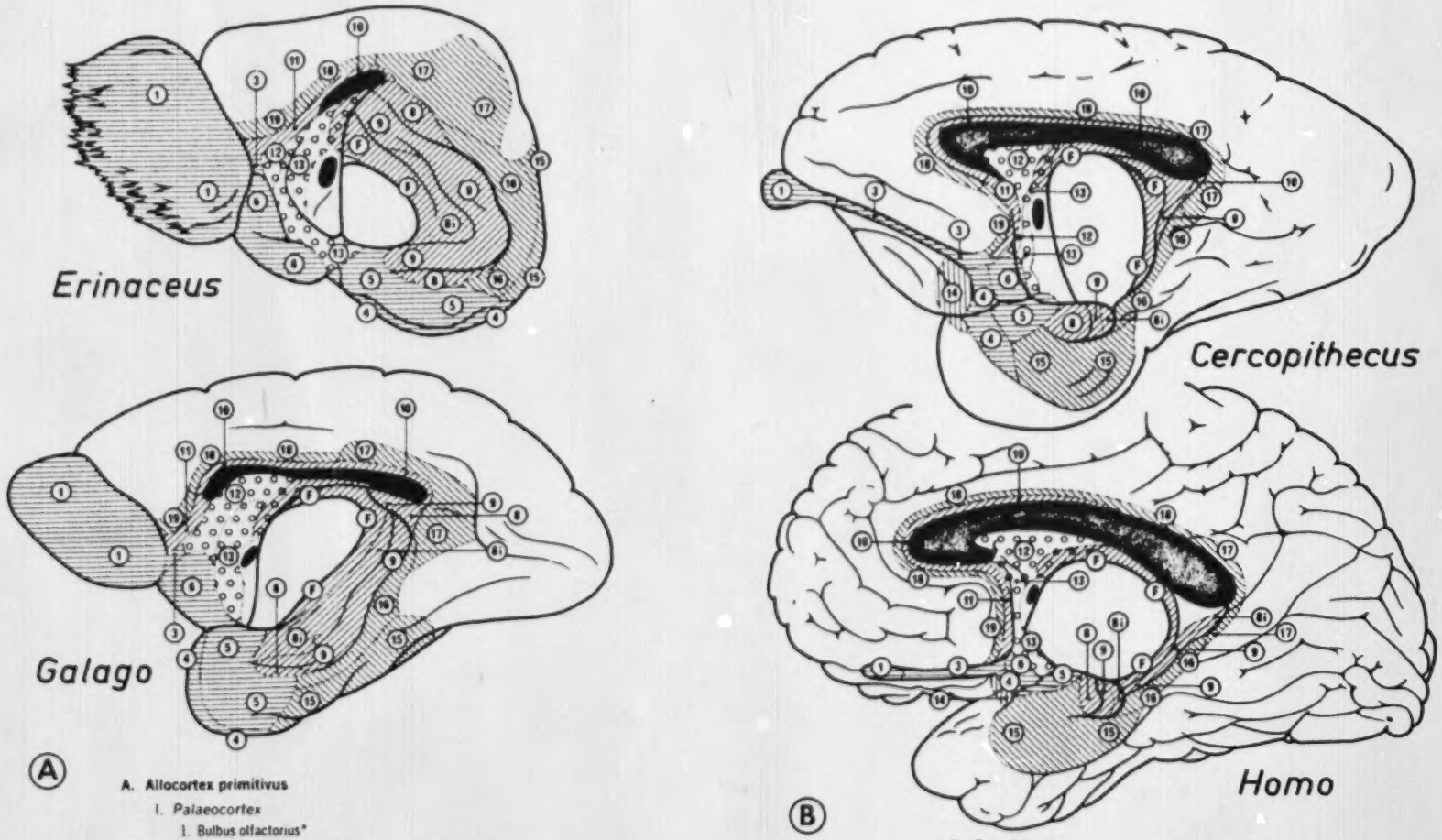


B. Reconstruction of human rhinencephalon as seen from above.

Amyg., amygdala; Ante. Comm., A.C., anterior commissure; Ante., anterior nucleus of thalamus; Bulb, olfactory bulb; Comm. Hipp., hippocampal commissure; Dent.G., dentate gyrus; Diag. Bd., diagonal band; Hab., habenula; Hap-ped., habenulopeduncular tract; Hipp., hippocampus; Iped., interpeduncular nucleus; Lat.St., lateral olfactory stria; Long. St., longitudinal stria; Mam. mammillary body; Med.St., medial olfactory stria; M.F.B., medial forebrain bundle; M.-th., mammillothalamic tract; St.Med., stria medullaris; St.Term., stria terminalis; Subcal., subcallosal gyrus; Tract., olfactory tract; Tub., olfactory tubercle.



Medial views of the telencephalon in *Erinaceus*, *Galago*, *Cercopithecus*, and *Homo*, showing the position and shape of the various allocortical regions in representatives of the ascending primate scale. Commissures are in black. F Fornix, 8 i Cornu ammonis inversus (Sanides, 1970:116-117).



A. Allocortex primitivus

I. *Palaeocortex*

1. Bulbus olfactorius*
2. Bulbus olfactorius accessorius*
3. Regio retrobulbaris (=nucleus olfactorius anterior)*
4. Regio praepirriformis (Area 51 of Brodmann)
5. Regio periamygdalaris
6. Tuberculum olfactorium

II. *Archicortex* (Hippocampus, Formatio ammonis)

7. Subiculum } Hippocampus retro commissuralis
8. Cornu ammonis } Hippocampus retro commissuralis
9. Fascia dentata } Hippocampus retro commissuralis
10. Hippocampus supracommissuralis } Taenia tecta of Rose
11. Hippocampus praecommissuralis } Taenia tecta of Rose

Structures with uncertain affiliation

12. Septum*
13. Diagonal band of Broca (Regio diagonalis)*

B. Periallocortex

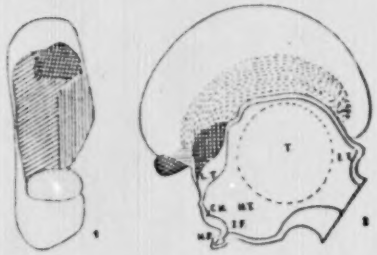
III. *Peripalaeocortex*

14. Formatio mesocorticalis insularis
    a. oralis (15 Brodmann)
    b. caudalis } (16 Brodmann)
    c. temporalis } (16 Brodmann)

IV. *Periarchicortex*

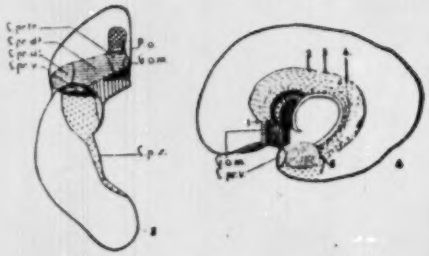
15. Regio entorhinalis + perrirhinalis (28, 34, 35 Brodmann)
16. Regio praesubicularis + parasubicularis (27 Brodmann)
17. Regio retrosplenialis (26, 29, 30 Brodmann)
18. Regio infraradiata ventralis (33 Brodmann)
19. Regio subgenualis posterior (caudale 25 Brodmann, 14 b Vogt)

Figs. 1 to 10 These are diagrams showing the olfactory areas in the telencephalon (i.e., rhinencephalon) of human fetuses at successive stages of development. All are drawn at the same size in order to show the relative proportions of the areas in the different stages.



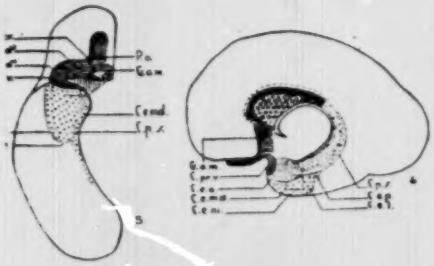
STAGE 1

. 1 and 2 Ventral and median views of the human brum at the end of the second month of fetal age.



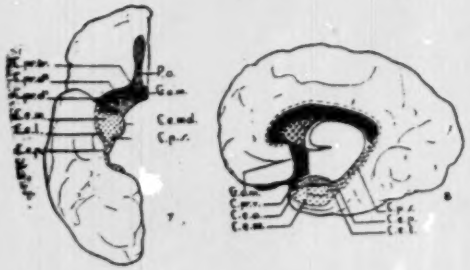
STAGE 2

Figs. 3 and 4 Ventral and median views of the human cerebrum at the end of the third month. The 4 subdivisions of the hippocampal formation lie respectively between the nos. 1 and 2, 2 and 3, 3 and 4, 4 and 5.

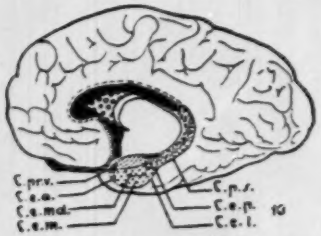


STAGE 3

;. 5 and 6 Ventral and median views of the human ebrum at the end of the 4th month.



Figs. 7 and 8 Ventral and median views of the human cerebrum at the end of the 6th month.



Figs. 9 and 10 Ventral and median views of the new-born human cerebrum.

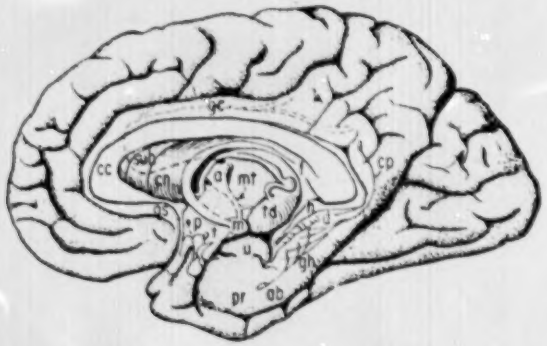
KEY TO THE SYMBOLS OF FIGURES 1 TO 10

- BULBO-PEDUNCULAR EMINENCE
  OLFACTORY BULB
- PREPIRIFORM AREA
- GYRUS OLFACTORIUS MEDIALIS
  OLFACTORY PEDUNCLE: PREPIRIFORM AREA
- PAROLFACTORY TUBERCLE
- VENTRAL PAROLFACTORY AREA
  BASAL PAROLFACTORY SPACE
- MEDIAL PAROLFACTORY AREA
- ENTORHINO-AMYGDALOID AREA
  ENTORHINAL AND PRESUBICULAR CORTEX
- CORTICAL AMYGDALOID NUCLEUS
- HIPPOCAMPAL AREA
  AMMON'S HORN
- FASCIA DENTATA
- PRIMORDIUM HIPPOCAMPI
- SEPTUM PELLUCIDUM
- ANTERIOR COMMISSURE
  HIPPOCAMPAL COMMISSURE
  CORPUS CALLOSUM

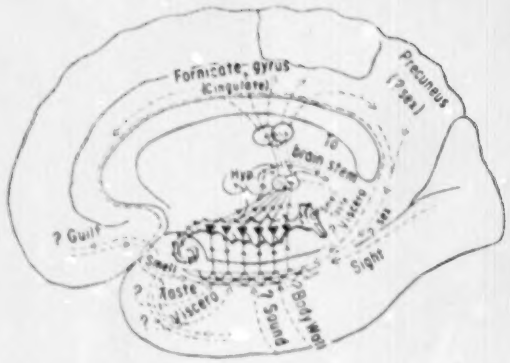
ABBREVIATIONS FOR ALL FIGURES

A.A., anterior amygdaloid area
A.C.L., claustro-amygdaloid area
A.D., diagonal area
A.g.b., undifferentiated basal ganglia
A.I., intercalated area
Al., alveus
B., basal amygdaloid nucleus
B.n.s., bed nucleus of stria terminalis
C., central amygdaloid nucleus
C.A., anterior commissure
Ca., Ammon's horn
Ca.n., caudate nucleus
C.C., corpus callosum
C.E., entorhinal cortex
C.e., external capsule
C.e.a., entorhinal cortex, anterior field
C.e.l., the same, lateral field
C.e.m., the same, middle field
C.e.md., the same, medial field
C.e.p., the same, posterior field
C.H., chiasma opticum
C.p., pyramidal cells
C.p.a., preambicular cortex
C.pr.d'., prepiriform cortex, subinsular zone
C.pr.d'., the same, gyrus olfactorius lateralis
C.pr.tr., the same, olfactory trigone
C.pr.v., the same, ventral zone
C.prp.i., undifferentiated prepiriform cortex
Cl.d., dorsal claustrum
Cl.f., claustrum falsum
Cl.v., ventral claustrum
E.T., epithalamus
F., fimbria
F.d., fascia dentata
F.H., hippocampal fissure
G.o.m., gyrus olfactorius medialis
G.P. or G.p., globus pallidus
H., hippocampus
H.P., hypophysis
H.T., hypothalamus
H.U., uncus s. hippocampus
I., insula
I.F., infundibulum
I.L.Ca., Ammon's horn, lamina centralis
H.L.Ca., the same, lamina dorsalis
III.L.Ca., the same, lamina terminalis
L., lateral amygdaloid nucleus
L.T., lamina terminalis
M., medial amygdaloid nucleus
M.o.p.s., germinative layer of paliostriatal angle
M.g., germinative layer of basal ganglia
M.p., germinative or periventricular layer
N., neopallial cortex
N.a., nucleus accumbens
N.c., cortical amygdaloid nucleus
N.C.A., anterior part of N.c.
N.C.P., posterior part of N.c.
P., putamen
P.H., primordium hippocampi
P.H.s., the same, pars supracallosa
P.l.n., lateral parolfactory (septal) nucleus
P.m.n., medial parolfactory (septal) nucleus
P.o., olfactory peduncle
P.sub., preambicular cortex
P.t., parolfactory tubercle
P.v.a., ventral parolfactory area
Pl.c., choroid plexus
Pr.a., preambicular cortex
S.A., or S.a., fissura amygdaloidea
S.H.t., septo-hippocampal tract
S.I., innominate gray matter
S.p., septum pellucidum
S.t.tr., septo-tubercular tract
Sg., granular layer of fascia dentata
Sp., polymorphic layer of fascia dentata
St.c., cortical plate
St.g., germinative or periventricular layer
St.i., intermediate layer
St.m., marginal layer
Sub., subicular cortex
T., thalamus
V.L. or V.l., lateral ventricle
V.T., V.t., ventricle of temporal lobe

ILLUSTRATION OF FOUR 'CLASSIC' PROPOSALS
FOR DEFINING THE LIMBIC SYSTEM AS A FUNCTIONAL ENTITY



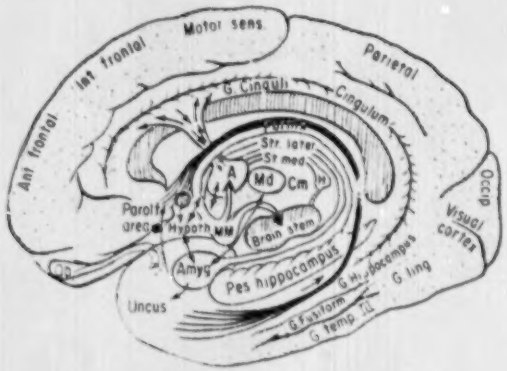
A



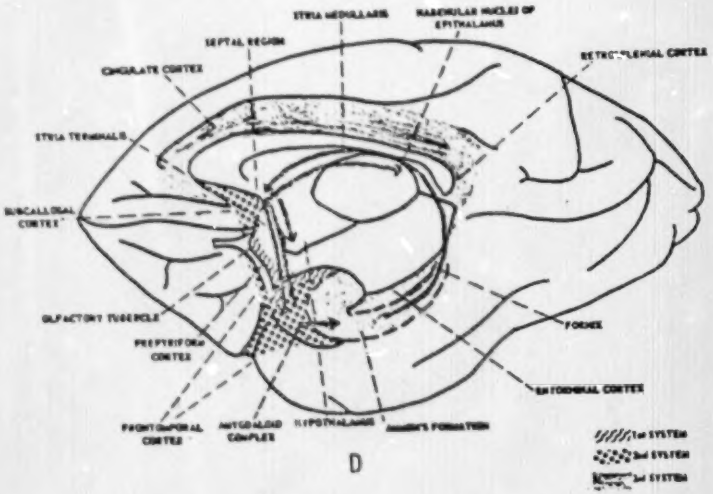
B

A The original proposal of Papez (1937) establishing the role of limbic structures in emotional behavior. Abbreviations: a, anterior nucleus; ab, angular bundle; cc, corpus callosum; cn, caudate nucleus; cp, posterior cingulum; d, dentate gyrus; f, fornix; gc, cingulate gyrus; gh, hippocampal gyrus; gs, subcallosal gyrus; h, hippocampus nudus; m, mammillary body; mt, mammillothalamic tract; p, pars optica of the hypothalamus; pr, pyriform area; sub, subcallosal bundle; t, tuber cinereum; td, mammillotegmental tract; th, hypophyseal tract; u, uncus.

B The modified version presented in MacLean (1949)



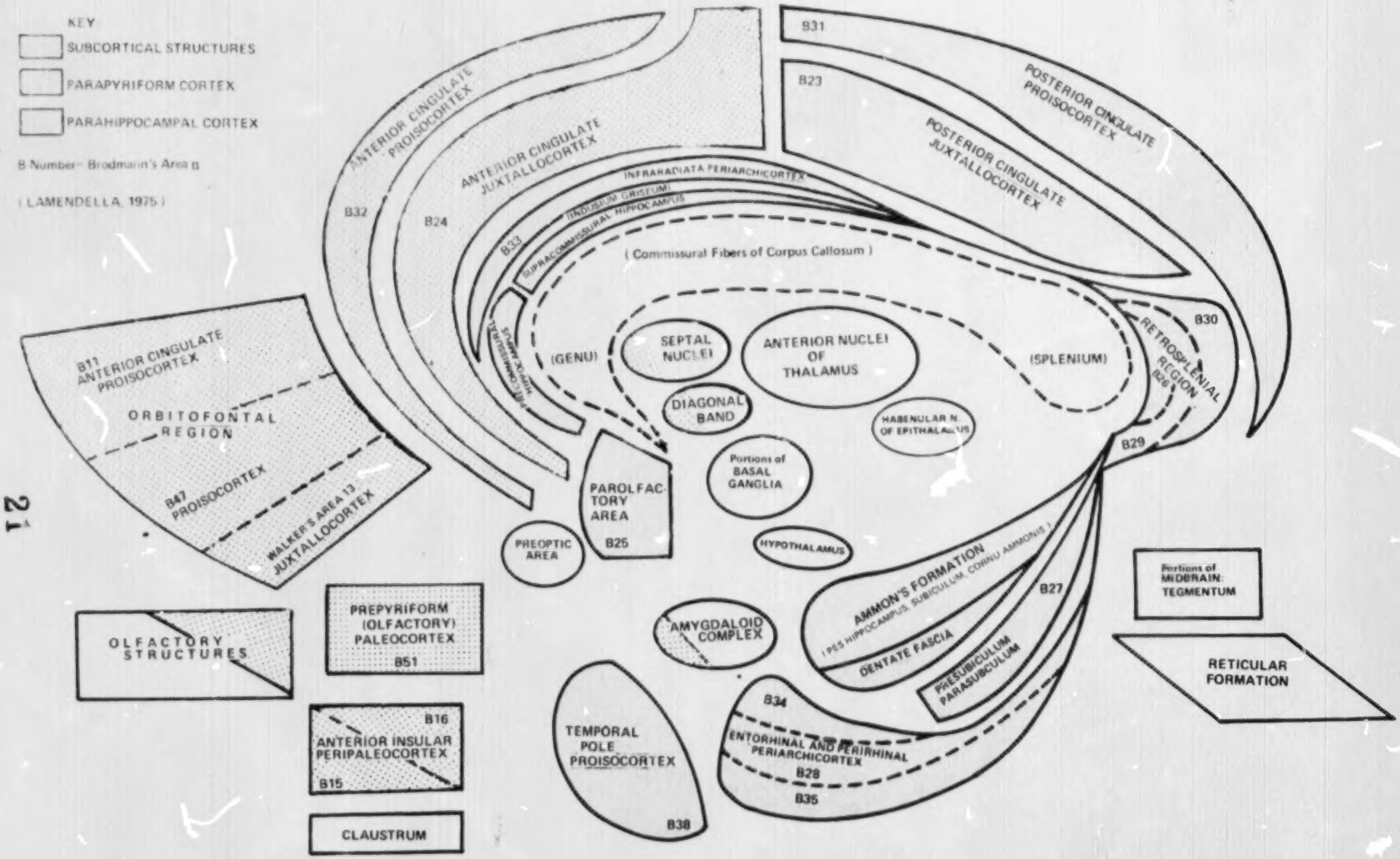
C



C The version presented by Penfield and Jasper (1954)

D The proposal of Pribram and Kruger (1954) dividing the rhinencephalon into three subsystems: (1) Rhinal System: structures having direct connections with the olfactory bulb; (2) Paleol System: structures having direct connections with the first system but none with the olfactory bulb; (3) Hippocampal-cingulate System: structures having direct connections with the second system but none with the bulb or first system.

SCHEMATIC DIAGRAM OF BRAIN STRUCTURES INVOLVED IN LIMBIC ACTIVITY



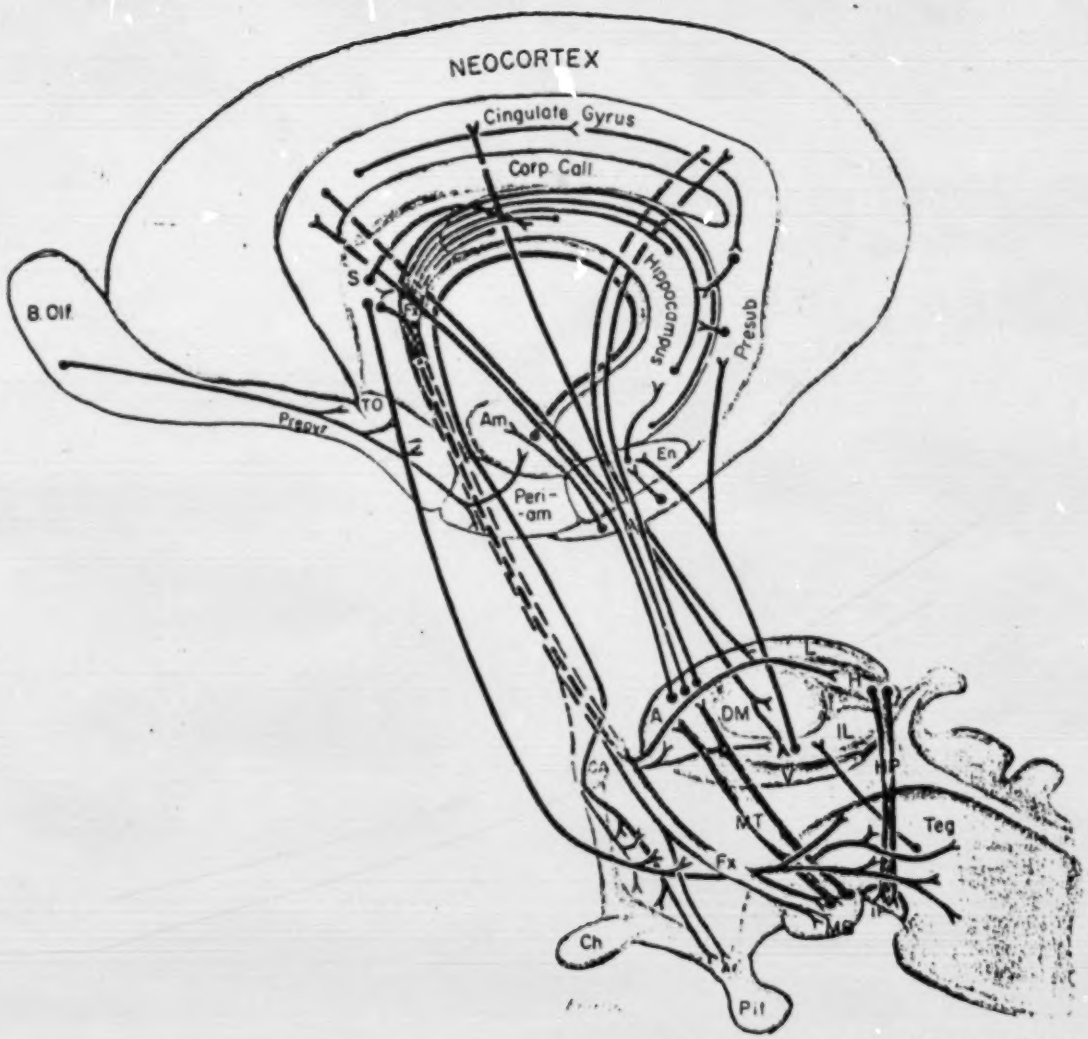
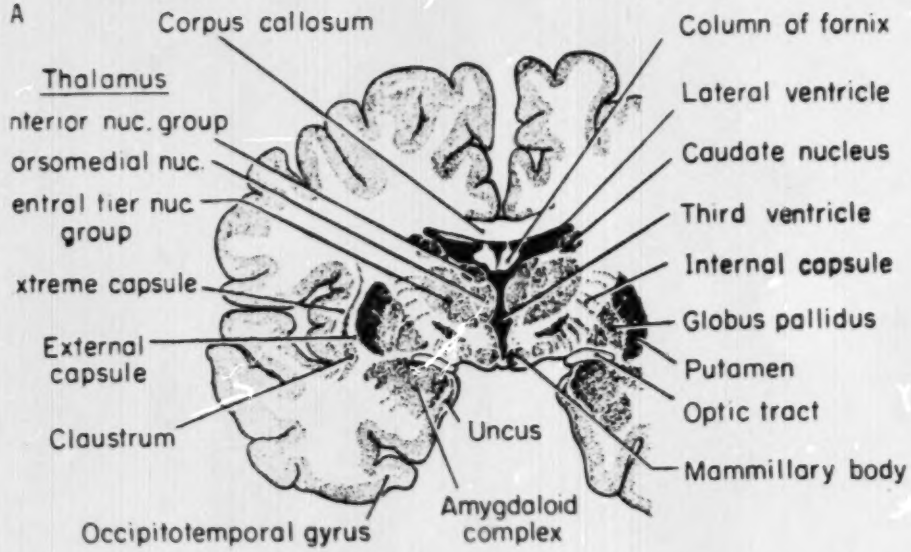


FIG. 30.1. Schematic diagram of the principal anatomical relationships between the allocortex, the juxta-allocortex, and the several subcortical structures considered in the present treatment of the limbic system. The brain-stem portions of the system have been schematically displaced from the lulus of the hemisphere and represented in the lower half of the illustration in order to facilitate visualization of the numerous anatomical interconnections involving these structures. Abbreviations: *A*, anterior nucleus of the thalamus; *Am*, amygdaloid complex; *Ar*, arcuate nucleus; *B. Olf.*, olfactory bulb; *CA*, anterior commissure; *Ch*, optic chiasm; *Corp. Call.*, corpus callosum; *DM*, medial dorsal nucleus of the thalamus; *En*, entorhinal area; *Fx*, fornix; *H*, habenular complex; *HP*, habenulo-interpeduncular tract; *IL*, intralaminar thalamic nuclei; *IP*, interpeduncular nucleus; *L*, lateral thalamic nucleus; *MB*, mammillary body; *MT*, mammillothalamic tract; *Peram*, peramygdaloid cortex; *Pit*, pituitary; *Prepyr*, prepyriform cortex; *Presub*, presubiculum; *S*, septal region; *Teg*, midbrain tegmentum; *TO*, olfactory tubercle; *V*, ventral nucleus of the thalamus. (Russell, 1961: 414).

COMPONENTS OF THE LIMBIC SYSTEM: AMYGDALOID COMPLEX

A

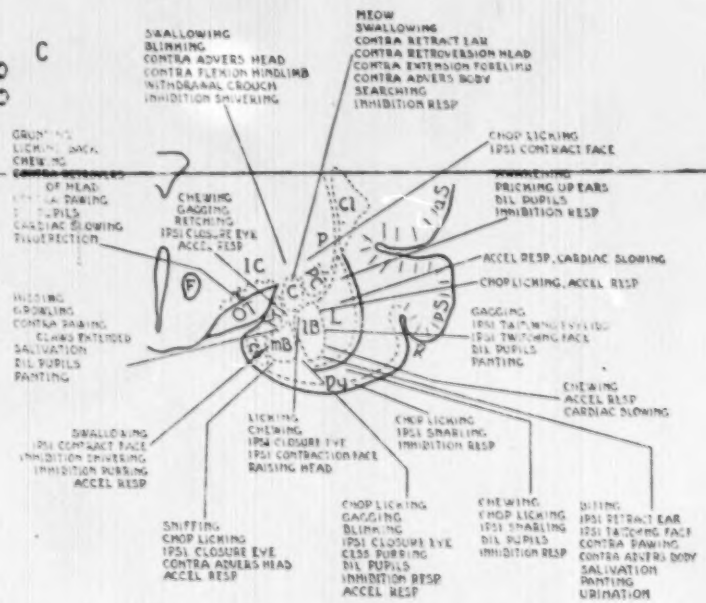


A Frontal section of the brain passing through the level of the mammillary bodies. In this section main nuclear groups of the thalamus are evident, as well as both segments of the globus pallidus and the thalamic nucleus. The amygdaloid nuclear complex lies medial to the uncus and below the lenticular nucleus. (Truex and Carpenter, 1969:501)

B Selected studies of effects of electrical stimulation in the amygdala of the cat (Egger and Flynn, 1967:180)

Experimenters	*Sites of stimulation tending to be in dorsomedial amygdala*	*Sites of stimulation tending to be in lateral and ventral amygdala*
Egger and Flynn, 1963	Suppression of hypothalamically elicited attack behavior	Facilitation of hypothalamically elicited attack behavior
Fernandez de Molina and Hunsperger, 1959	Growling, hissing	Sniffing, retching
Gastaut, 1952; Morin *et al.*, 1952	Increased blood pressure	Decreased blood pressure
Hilton and Zbrożyna, 1963; Zbrożyna, 1963	Defense reaction, including growling and extension of claws	Sniffing, searching
Kaada, 1951	Inhibition of knee jerk and of cortically induced movements	Facilitation of knee jerk and of cortically induced movements
Koikegami and Fuse, 1952	Increased amplitude of respiration	Decreased amplitude of respiration
Koikegami *et al.*, 1952	Inhibition of gastrointestinal motility	Rise in body temperature
Kreindler and Steriade, 1964	Acceleration-desynchronization of neocortical electrical activity	Synchronization of neocortical electrical activity in the form of spindles and slow waves
MacLean and Delgado, 1953	Respiratory acceleration	Respiratory inhibition
Magnus and Lammers, 1956	Growling	Mastication
Norris, Jr., 1963	Arrest of eating and mousing, arousal	Effects other than arrest of activity or arousal
Shealy and Peele, 1957	Undirected rage	Cowering, sniffing, licking
Slusher and Hyde, 1961	Increased corticosteroid levels in adrenal vein	Decreased corticosteroid levels in adrenal vein
Ursin and Kaada, 1960	Growling and hissing	Cowering, flight, searching
~~Wood, 1958~~	~~Respiratory acceleration,~~ growling and biting	~~Respiratory inhibition, searching~~
Yoshida, 1963	Rage	Sneezing, seeking
Zbrożyna, 1963	Inhibition of firing in short ciliary nerve, with dilation of sympathectomized pupil	Facilitation of firing in short ciliary nerve

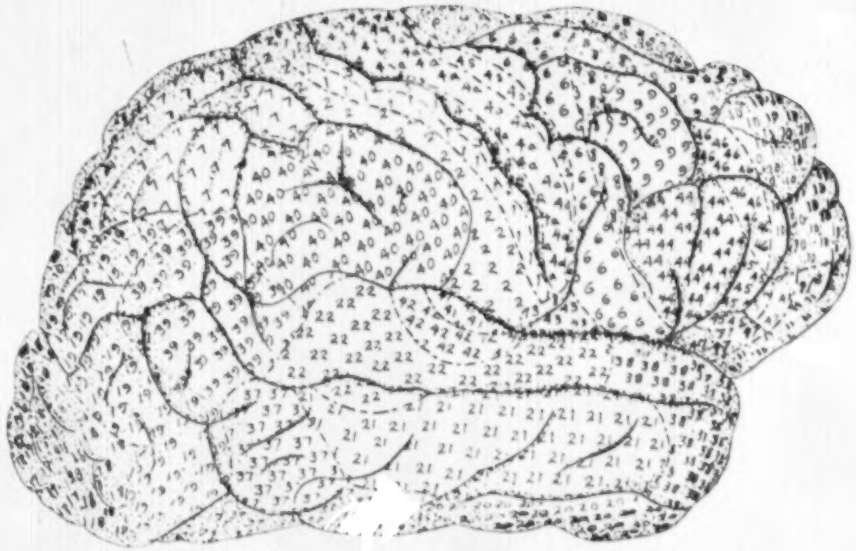
C



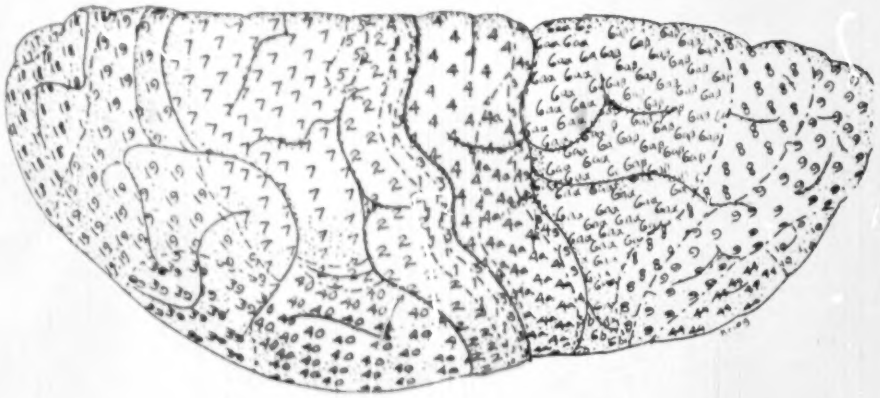
C Cross section through midregion of amygdala showing types of oral, facial and other behavior resulting from stimulation. Note the divisions of the amygdala and its relationship to other brain structures. Abbreviations: *LB* and *mB*, lateral and medial parts of basal nucleus of amygdala; *L*, lateral nucleus; *C*, central nucleus of amygdala; *F*, fornix; *OT*, optic tract; *Py*, pyriform cortex; *R*, rhinal fissure; *Cl*, claustrum; *P*, pulvinar; *IC*, internal capsule; *Co*, cortical nucleus of amygdala; *E*, entopeduncular nucleus; *M*, medial nucleus of amygdala; *PC*, putamen-central amygdaloid complex; *aS*, anterior sylvian gyrus; *pS*, posterior sylvian gyrus. (From MacLean and Delgado, *Electroenceph. clin. Neurophysiol.*, 1953, 5:91–100.)

BRODMANN'S CLASSIFICATION OF THE CEREBRAL CORTEX

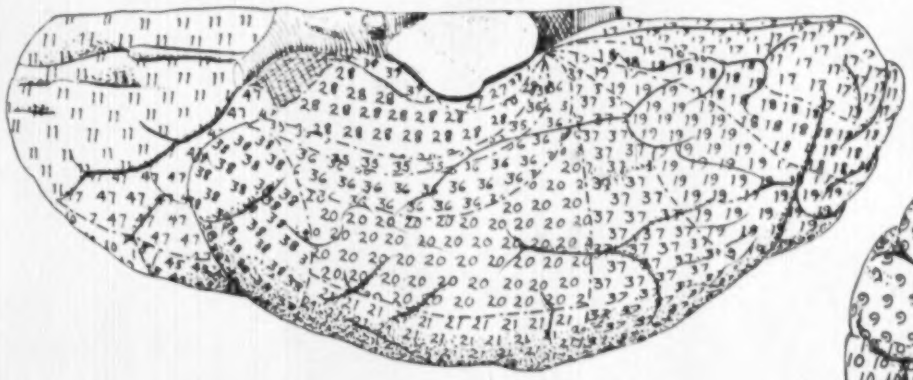
(Adapted from Krieg, 1966:366-367)



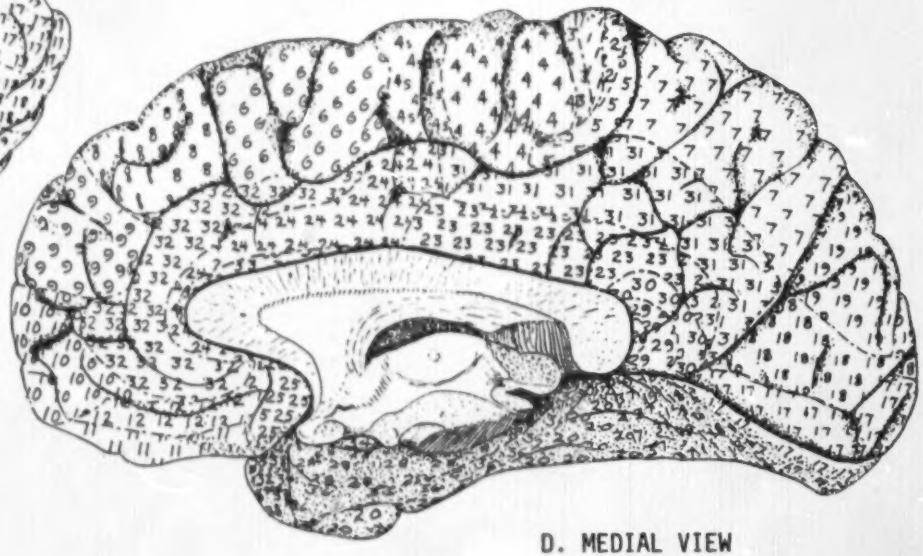
A. LATERAL VIEW



B. DORSAL VIEW



C. BASAL VIEW



D. MEDIAL VIEW

AN EXAMPLE OF A VOCALIZATION TYPE (CACKLING)
ELICITED BY ELECTRICAL STIMULATION OF THE BRAIN IN SQUIRREL MONKEYS
(Adapted from Jürgens and Ploog, 1970)

Squirrel monkeys produce cackling calls in situations characterized by general aggressiveness and high excitement; cackling is usually uttered by several animals simultaneously. For this study, all vocalizations consisting of a sequence of two or more elements at intervals of 81 ± 19 msec and with a maximum intensity below 2000 cps were defined as cackling calls. A schematic representation of the spectral pattern of cackling calls is given in Figure 1.

Figure 1

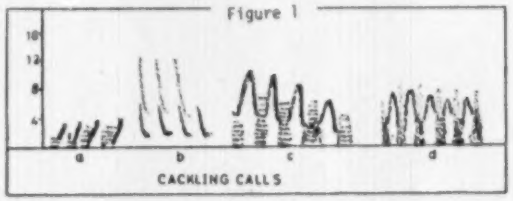


Figure 2 shows the electrode positions yielding cackling calls in a series of representative frontal planes according to stereotaxic coordinates. These positions form a continuous system, illustrated in Figure 3, outside of which no cackling calls can be elicited. This system runs from the caudal end of the periaqueductal grey and adjacent parabrachial nuclei (AP -1) in a periaqueductal and periventricular position, respectively, throughout the midbrain and diencephalon (AP -1 to AP 9.5). At the level of the inferior thalamic peduncle the system branches off in three components: the first component follows the inferior thalamic peduncle in a dorsal direction towards the anteromedial peduncle ventrolaterally into the central and basal nuclei of the amygdala (AP 10.5 to AP 8.5) and farther through the external capsule and uncinate fasciculus (AP 10.5) to the rostroventral temporal cortex (AP 13.5); the third component follows the anterior thalamic radiation along the ventromedial border of the internal capsule (AP 9.5 to AP 16.5) into the ventromedial orbital cortex (AP 16.5) and precallosal cingulate gyrus (AP 20).

Figure 2

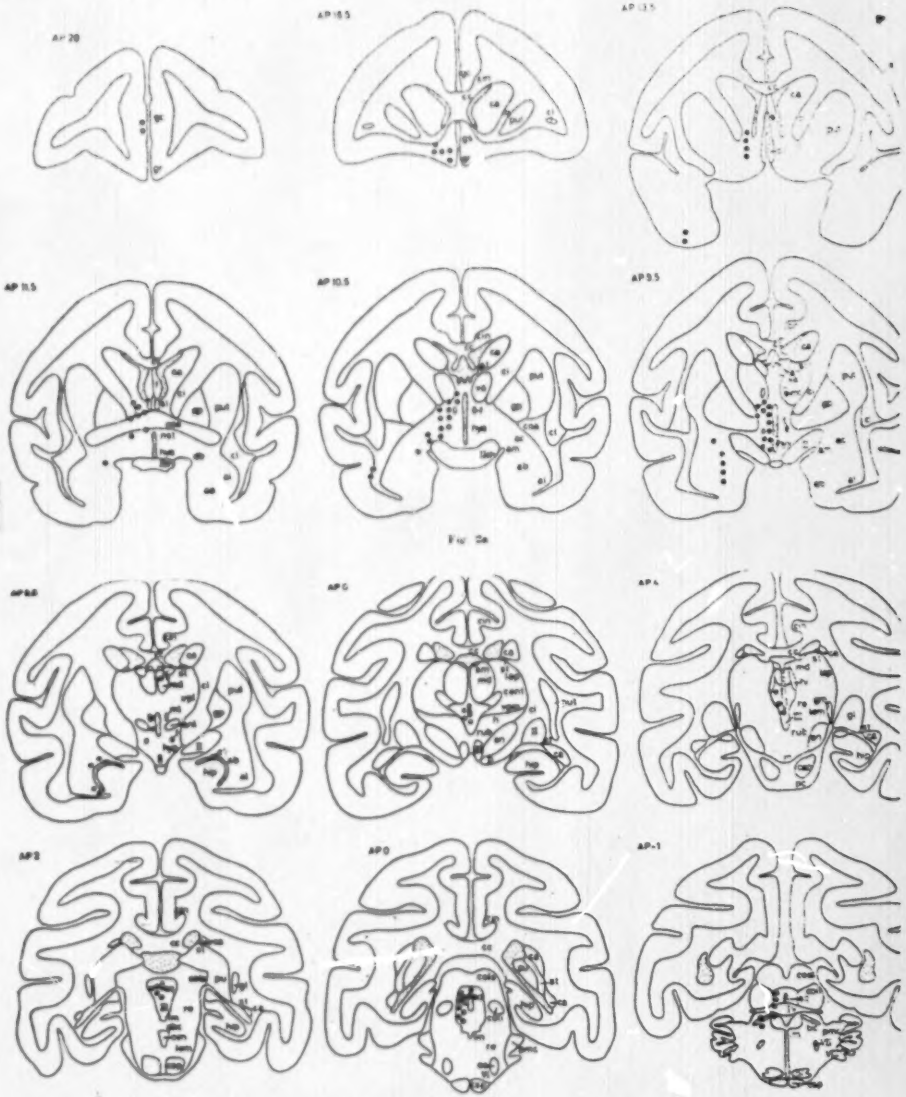


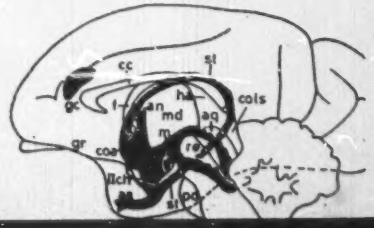
Fig. 2a

Fig. 2b

Abbreviations

a:	Nucl. accumbens
aa:	Area anterior amygdalae
ab:	Nucl. basalis amygdalae
ac:	Nucl. centralis amygdalae
al:	Nucl. lateralis amygdalae
am:	Nucl. medialis amygdalae
an:	Nucl. anterior thalami
anl:	Ansa lenticularis
aq:	Substantia grisea centralis
bc:	Brachium conjunctivum
ca:	Caudatum
cc:	Corpus callosum
cen:	Nucl. centralis superior (Bechterew)
cent:	Centrum medianum
ci:	Capsula interna
cin:	Cingulum
cl:	Claustrum
coa:	Commissura anterior
coli:	Colliculus inferior
cols:	Colliculus superior
cr:	Corpus restiforme
csp:	Tr. corticospinalis
db:	Fasc. diagonalis Broccae
dbc:	Decussatio brachii conjunctivi
f:	Fornix
gc:	Gyrus cinguli
gr:	Gyrus rectus
gs:	Gyrus subcallosus
h:	Campus Foreli
ha:	Nucl. habenularis
hi:	Tr. habenulointerpeduncularis
hip:	Hippocampus
hya:	Area hypothalamica anterior
hyp:	Area hypothalamica posterior
hyv:	Area hypothalamica ventralis
in:	Nucl. interpeduncularis
lap:	Nucl. lateralis posterior thalami
lav:	Nucl. lateralis ventralis thalami
le:	Lemniscus lateralis
lem:	Lemniscus medialis
lm:	Fasc. longitudinalis medialis
m:	Corpus mamillare
md:	Nucl. medialis dorsalis thalami
mf:	Tr. mamillothalamicus
nd:	Nucl. striae terminalis
ni:	Nucl. olivaris inferior
ol:	Fasc. olfactorius (Zuckerkandl)
os:	Nucl. olivaris superior
p:	Pedunculus cerebri
pmc:	Brachium pontis
po:	Griseum pontis
pp:	Nucl. praepositus hypoglossi
put:	Putamen
re:	Formatio reticularis tegmenti
rep:	Nucl. reticularis tegmenti pontis
rl:	Nucl. reticularis lateralis myelencephali
rub:	Nucl. ruber
s:	Septum
sm:	Stria medullaris
sn:	Substantia nigra
st:	Stria terminalis
sto:	Stria olfactoria lateralis
tec:	Tr. tegmentalis centralis
trz:	Corpus trapezoides
va:	Nucl. ventralis anterior
vpl:	Nucl. ventralis posterolateralis thalami
vpm:	Nucl. ventralis posteromedialis thalami
zi:	Zona incerta
II:	Tr. opticus
IICh:	Chiasma nervorum opticorum
III:	N. oculomotorius Nucl. nervi oculomotorii
IV:	N. and Nucl. nervi trochlearis
VI:	N. abducens
VII:	N. facialis

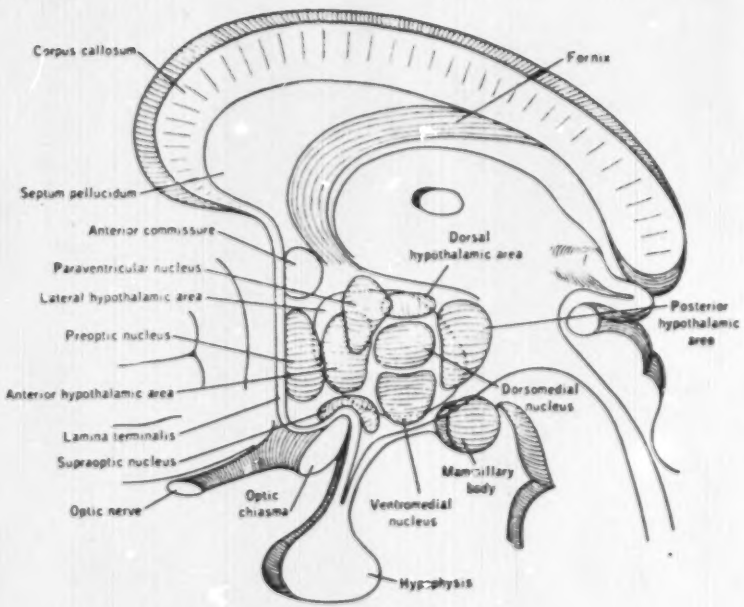
Figure 3



General (sagittal) view of the cerebral system yielding cackling calls

COMPONENTS OF THE LIMBIC SYSTEM: HYPOTHALAMUS

A



A Three dimensional reconstruction of the Hypothalamus (From Pribram, 1971:186, taken from House and Pansky, 1967).

B

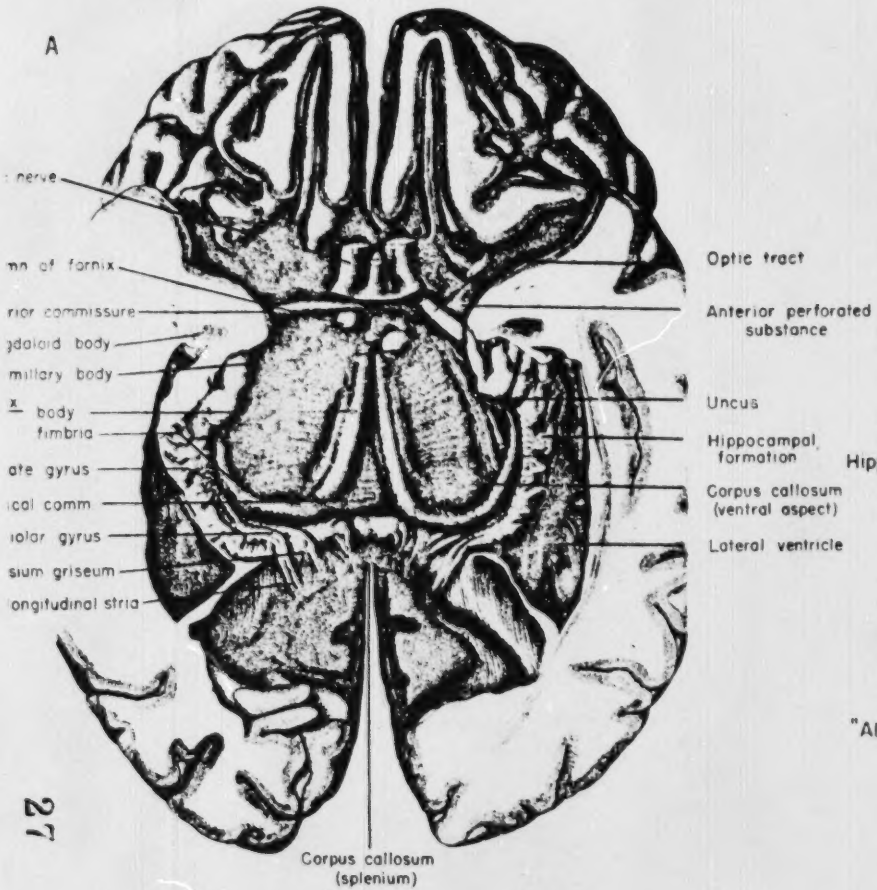
Summary of hypothalamic regulatory mechanisms.*

Function	Afferents From	Integrating Centers
Temperature regulation	Cutaneous cold receptors; temperature-sensitive cells in hypothalamus	Anterior hypothalamus, response to heat; posterior hypothalamus, response to cold
Neuroendocrine control of:		
Catecholamines	Emotional stimuli, probably via limbic system	Dorsomedial and posterior hypothalamus
Vasopressin	Osmoreceptors, "volume receptors," others	Supraoptic nuclei
Oxytocin	Touch receptors in breast, uterus, genitalia	Paraventricular nuclei
Thyroid-stimulating hormone (TSH)	Temperature receptors, perhaps others (?)	Anterior median eminence and anterior hypothalamus
Adrenocorticotropic hormone (ACTH)	Limbic system (emotional stimuli); ascending reticular system ("systemic" stimuli); hypothalamic or anterior pituitary cells sensitive to circulating blood corticosteroid level; others (?)	Middle portion of median eminence
Follicle-stimulating hormone (FSH) and luteinizing hormone (LH)	Hypothalamic cells sensitive to estrogens; eyes, touch receptors in skin and genitalia of reflex ovulating species	Posterior median eminence, other areas
Prolactin	Unknown receptors	Posterior median eminence (hypothalamus inhibits secretion)
Growth hormone	Unknown receptors	Anterior median eminence
"Appetitive" behavior		
Thirst	Osmoreceptors	Lateral superior hypothalamus
Hunger	"Glucostat" cells sensitive to rate of glucose utilization	Ventromedial satiety center, lateral hunger center, also limbic components
Sexual behavior	Cells sensitive to circulating estrogen and androgen, others	Anterior ventral hypothalamus plus, in the male, piriform cortex
Defense reactions (fear, rage)	Sense organs and neocortex, paths unknown	Diffuse, in limbic system and hypothalamus

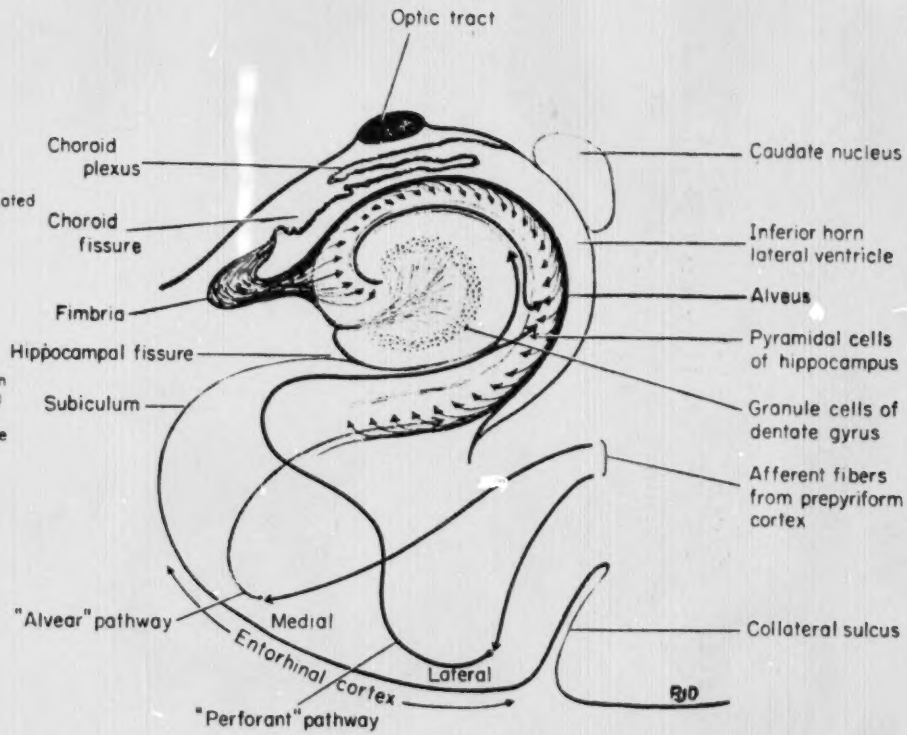
*Reproduced, with permission, from Ganong WF: *Review of Medical Physiology*, 5th ed. Lange, 1971.

COMPONENTS OF THE LIMBIC SYSTEM: HIPPOCAMPUS AND RELATED STRUCTURES

A



B

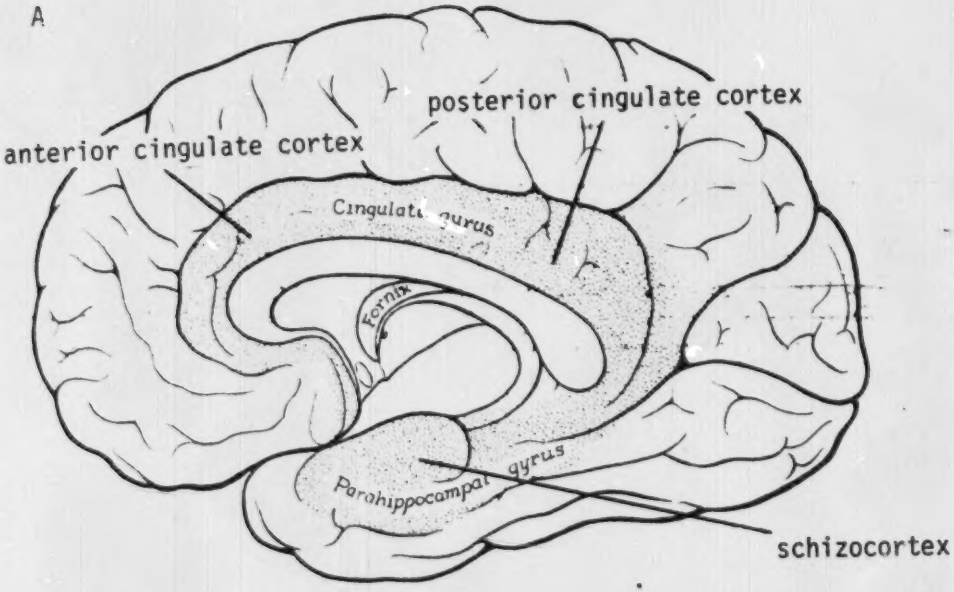


A Dissection of the inferior surface of the brain showing the configuration of the fornix, the hippocampal formation, the dentate gyrus, and related structures (Adapted from Mettler, 1948).

B Semischematic diagram of the hippocampal formation, dentate gyrus and entorhinal area. In the dentate gyrus only the granular layer is indicated. In the hippocampal formation only pyramidal cells and their axons projecting into the alveus are shown. Afferent fibers from prepyriform cortex projecting to the entorhinal cortex are shown in *black*. Projections of the entorhinal cortex to the hippocampal formation follow two pathways: (1) the lateral region gives rise to fibers which follow the so-called "perforant" pathway (*red*), and (2) the medial region gives rise to fibers which follow the so-called "alvear" pathway (*blue*). Axons of pyramidal cells in the hippocampal formation entering the alveus pass to the fimbria of the hippocampus. The dentate gyrus gives rise to fibers that project only to the hippocampal formation. (Based on Lorente de Nó, '34, and a schematic diagram by Peele, '61.)

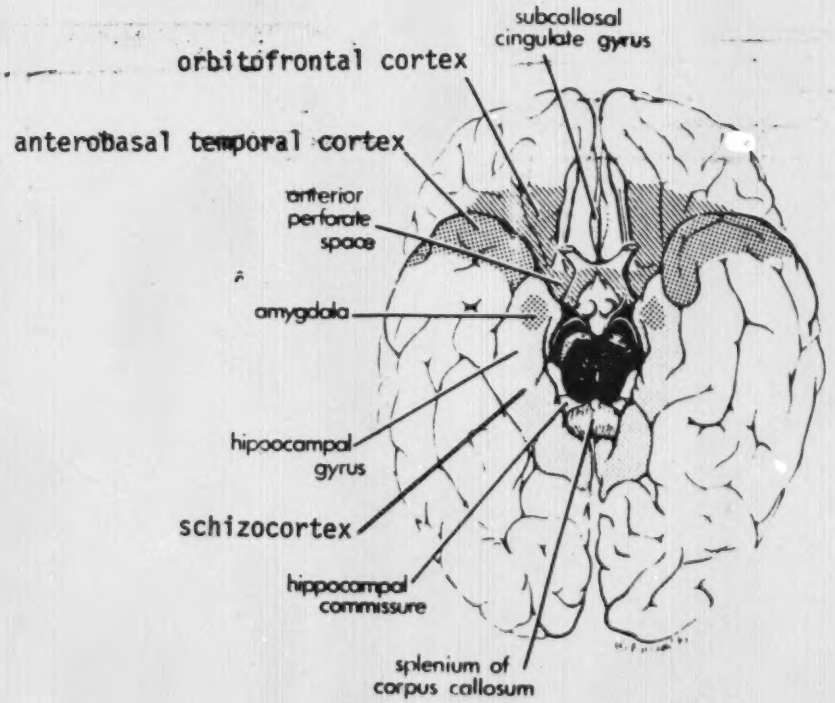
COMPONENTS OF THE LIMBIC SYSTEM: LIMBIC CORTEX

A



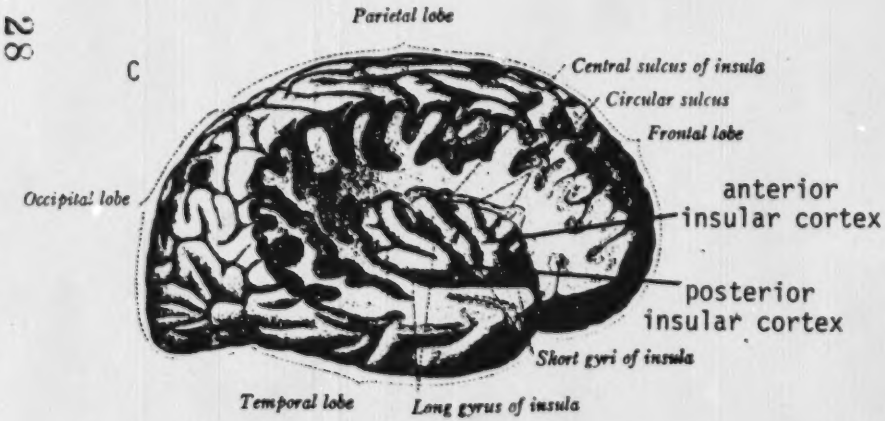
A View of the medial surface of the hemisphere showing "*le grand lobe limbique*" of Broca (1878) surrounding the hilus of the cerebral hemisphere (Adapted from Truex and Carpenter, 1969:539).

B



B Cortical regions of the limbic system as seen from below. Notice that in the horizonal plane the limbic cortex forms a "limbus" encircling the brain stem (Adapted from Livingston and Escobar, 1971:19).

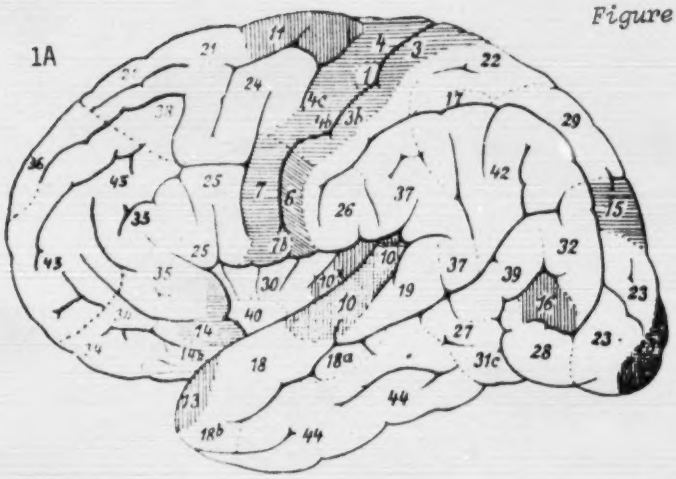
C



C Lateral view of the human cerebral hemisphere with the insula exposed by removal of temporal and parietal opercula (Adapted from Ranson and Clark, 1959:59).

Figure 1

1A



1B

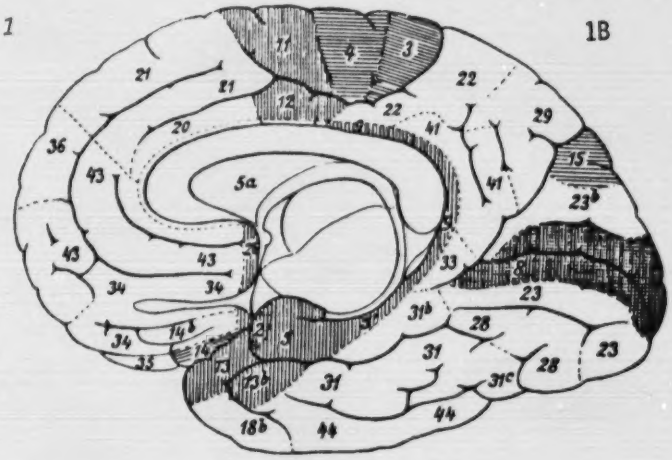


Figure 1. Flechsig's maps of myelinogenesis on the lateral surface (1A) and the medial surface (1B) of the human brain. In the view shown in 1A, the Sylvian fissure is opened so as to expose the insula. The myelinogenetic areas are numbered in the order in which they myelinate, No. 1 being the earliest and No. 45 the last. The hatched areas are the "primordial zones" which are myelinized at birth. The dotted areas are "intermediary zones" which myelinize between birth and one month after birth. The blank areas are the "terminal zones," the last areas of the cerebrum to myelinize. (Adapted from Flechsig, 1901)

Figure 2

2A

2B

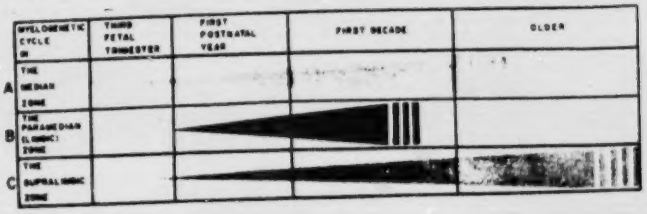


Figure 2A. A frontal section of the human brain showing three zones of the cerebral wall: (1) *Median zone*, grey; (2) *Paramedian zone*, black; (3) *Dorsolateral zone*, diagonal hatching = supralimbic association areas, cross-hatching = the opercular and paralimbic areas.

Figure 2B. Graphs A, B, and C represent comparatively the cycles of myelinization of the respective myeloarchitectonic zones in the brain wall.

Abbreviations: Mth, Median thalamic zone; PMTh, Paramedian thalamic zone; DLTh, Dorsolateral (and posterior) thalamic zone; Fx, Fornix; Hppc, Hippocampus; HppcRd, Hippocampal Rudiment; HTh, Hypothalamus. (Adapted from Yakovlev and Lecours, 1967)

Figure 1

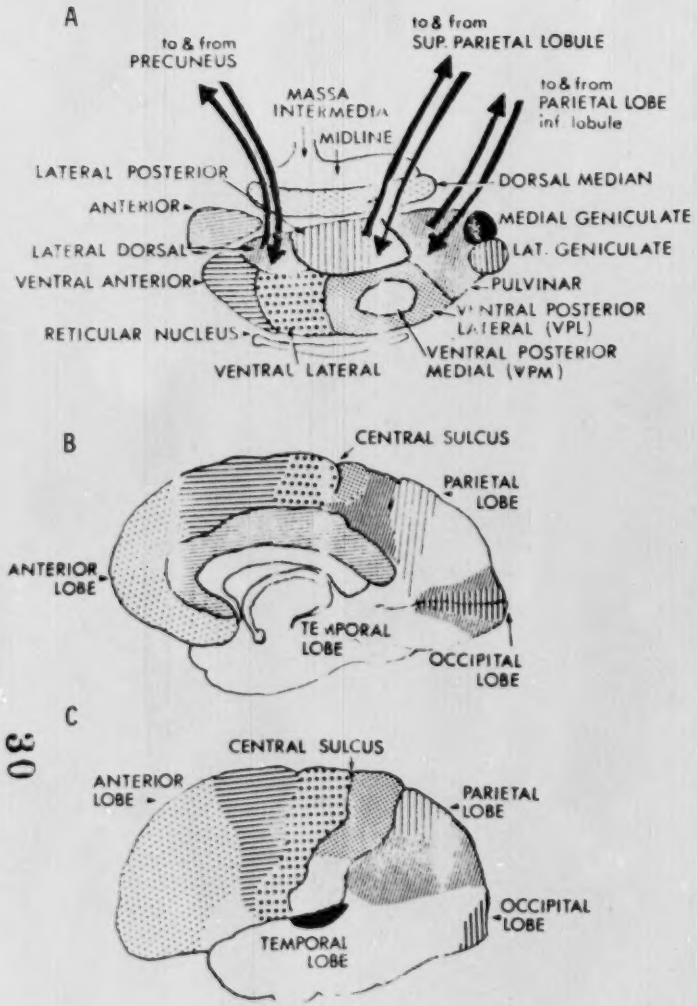


Diagram of the major thalamic nuclei (A) showing their thalamo-cortical projection areas on the medial surface (B) and the lateral surface (C) of the cerebral hemispheres (Adapted from Riklan and Levita, 1969:34, taken from Truex and Carpenter, 1964).

Figure 2

Patients undergoing bilateral thalamotomy as part of the treatment of Parkinson's disease were first observed during performance on a standard object-naming test while electrical stimulation was applied to the thalamus and medial parietal white matter. Stimulation in the left pulvinar nucleus of the thalamus and deep parietal white substance in the paracallosal region of both hemispheres produced *anomia* (name-finding difficulties). The photo below shows the left hemisphere of a right-handed patient sectioned 12 mm. from the mid-line. The lower section of the electrode tract is shown with three of the stimulus sites reconstructed. Anomia resulted from stimulation between the sites marked with arrows. The patient died of a massive right thalamic hemorrhage three weeks later, three days after coagulation in the right thalamus (Adapted from Ojemann, Fedio, and Van Buren, 1968).

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